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Metabolic rate models and the substitutability of predator populations

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Summary

1. Much of the debate surrounding the consequences of biodiversity loss centres around the issue of whether different species are functionally similar in their effects on ecological processes. In this study, we examined whether populations consisting of smaller, more abundant individuals are functionally similar to populations of the same species with larger, fewer individuals.
2. We manipulated the biomass and density of banded sunfish (*Enneacanthus obesus*) and measured their impact on populations of Southern leopard frog (*Rana sphenocephala*) larvae. We also evaluated the ability of models relating metabolic rate to body size to predict the relative impacts of populations that differ in average body size and population density.
3. Our results indicate that population biomass, density and their interaction each play a large role in determining the effect of a predator population on its food resource. Populations with smaller but more abundant individuals had effects as large or larger than those populations with larger but fewer individuals.
4. Although we found qualitative agreement between the observed relative effects of populations with that predicted by allometric models, we also found that density-dependence can cause effects of a population to differ from that expected based on allometry.
5. The substitutability of populations differing in average body size appears to depend on complex relationships between metabolic rate, population density and the strength of density-dependence. The restrictive conditions necessary to establish functional equivalence among different populations of the same species suggests that functional equivalence should be rare in most communities.

Key-words: allometry, body size, density dependence, functional equivalence, predation.

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Introduction

Predicting the impact of particular sets of species (e.g. trophic level, guild) within communities and ecosystems is a fundamental goal in ecology. Development of ecological models (e.g. Hairston, Smith & Slobodkin 1960; Menge & Sutherland 1976, 1987; Fretwell 1977; Oksanen *et al*. 1981; McQueen, Post & Mills 1986) has contributed substantially to our ability to make predictions and has been the impetus for many novel empirical studies. Most models, however, assume that different species within such sets are functionally similar (i.e. have substitutable effects). Furthermore, much debate surrounding the consequences of biodiversity loss centres around whether different species are functionally similar in their effects on various ecological processes. A growing body of work demonstrates that assumptions of functional similarity are not valid either for species within a trophic level (e.g. Morin 1983; Paine 1992; Kurzava & Morin 1998; McPeek 1998; Schmitz & Suttle 2001; Chalcraft & Resetarits 2003a) or populations within a species (reviews: Mills, Soule & Doak 1993 and Power *et al*. 1996).

Body size and abundance are factors that may cause species or populations to differ in impact. Although not true in all cases (e.g. Travis, Keen & Juilianna 1985; Chalcraft & Resetarits 2003b), larger organisms have a greater impact on food resources than smaller organisms (Paine 1976; Morin 1983; Peters 1983; Semlitsch & Gibbons 1988; Kurzava & Morin 1994; Babbitt &

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Tanner 1998). However, smaller species generally have higher densities (review: Brown 1995), smaller individuals of a species have higher densities (Yoda *et al*. 1963; White & Harper 1970; Morin 1983; Begon, Firbank & Wall 1986; Bristow 1991; Chalcraft 2002), and smaller size classes are generally more abundant within populations (Wilbur & Collins 1973; Wilbur 1984; Łomnicki 1988; review: Ebenman & Persson 1988). Often, different species or groups of species having similar biomass or density but different average body sizes are not substitutable (e.g. Morin 1983; Wilbur & Fauth 1990; Kurzava & Morin 1994, 1998; Hooper & Vitousek 1998; Ruesink 2000; Relyea 2001; Schmitz & Suttle 2001, Chalcraft & Resetarits 2003a; but see Morin 1995 for an exception). It remains unclear whether different populations of species are substitutable given the same circumstances (i.e. similar densities or biomasses). To understand better the relative importance of density and biomass in population effects on food resources, we first compared effects of different populations with different average body sizes but similar biomass or density.

Our second objective was to determine whether impacts of populations differing in average body size and density is predictable based on metabolic rate–body size relationships. Metabolic rate (MR) scales nonlinearly with body size (W):

$$\mathrm{MR} = aW^{b} \qquad \text{eqn 1}$$

where a and b are constants (Kleiber 1961; Peters 1983; Calder 1984; Schmidt-Nielsen 1984). Across species, b is consistently 0·75 while a varies with taxonomic group (Kleiber 1961; Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Brown 1995). Although some suggest that $b = 0{\cdot}67$ for intraspecific comparisons (Calder 1984; Schmidt-Nielsen 1984), Kleiber (1961) assumes it does not differ from interspecific comparisons. Total energy demand of a population (TED) with an average body size of W is:

$$\mathrm{TED}_{W} = \mathrm{MR} \times N \qquad \text{eqn 2}$$

where N is population density (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Brown 1995). Damuth (1981, 1987) proposed that different populations are energetically equivalent because the slope of the body size–metabolic rate relationship is equal in magnitude but opposite in sign to the body size–population density relationship. A formal mathematical representation indicates that populations will have equivalent TED when:

$$\frac{\ln\left(\frac{N_i}{N_j}\right)}{\ln\left(\frac{W_i}{W_j}\right)} = -b \qquad \text{eqn 3}$$

where b is as in (1) and i and j refer to the densities (N) and average body size (W) of populations i and j. The energetic equivalence rule has been subject to much debate among theoreticians (review: Brown 1995) but has received little attention from experimental ecologists. To date, only a single study (Ruesink & Srivastava 2001) has shown that effects of a group of consumers is proportional to its TED. If confirmed, this implies that relative effect of populations differing in body size and density should be predictable based on metabolic rate–body size relationships. Thus, some argue that groups of organisms may be substitutable if they have similar TED (i.e. are energetically equivalent) rather than similar density or biomass (Srivastava & Lawton 1998; Ruesink & Srivastava 2001).

Density-dependence is common in nature (review: Cappuccino & Price 1995). An important assumption in using TED to predict population effects, however, is that density-dependent effects on individual metabolic demands is minor as MR is measured on individuals. Hence eqn 1 has no density term modifying metabolic rate. This may limit the applicability of TED where strong density-dependence alters metabolic or consumption rates. Thus, our third objective was to evaluate how density might cause observed impacts of populations to differ from expectations based on TED.

Materials and methods

We conducted an experiment using 15 1100-L cattle tanks designed to mimic natural ponds (Morin 1983). Artificial ponds or mesocosms represent an important tool in experimental ecology (Wilbur 1987; Morin 1989, 1998; Fraser & Keddy 1997; Resetarits & Fauth 1998). Although scale is an important issue to consider in experiments employing mesocosms (Pearman 1993, 1995; Petersen & Hastings 2001), previous experiments and field studies in natural ponds suggest that many processes identified as important in artificial ponds function similarly in their natural counterparts (e.g. Petranka 1989; Scott 1990; Semlitsch *et al*. 1996; Resetarits & Fauth 1998).

Tanks were placed in an open field at the Naval Security Group Activity Northwest (NSGANW), east of the Great Dismal Swamp in extreme southeastern Virginia. Five experimental treatments were replicated in each of three spatial blocks. Predator-free control tanks contained only tadpoles (440/1000 L) of our target prey species, *Rana sphenocephala* Cope (Southern leopard frog), while four treatments also contained varying biomass and density of a predatory fish, *Enneacanthus obesus* Girard (Banded sunfish). *Enneacanthus* displayed the greatest range of body sizes and was one of the most abundant predators at NSGANW (Chalcraft & Resetarits 2003a). Furthermore, average body size and density of *Enneacanthus* are related inversely (Bristow 1991). Fish treatments differed in either biomass (3·5 g vs. 7 g of fish) or density (1/1000 L vs. 2/1000 L). *Rana* and *Enneacanthus* co-occur commonly throughout their geographical range (Kurzava & Morin 1998; Chalcraft, personal observation) and initial densities were within the range observed in natural ponds (Morin 1983, 1995; Bristow 1991; Kurzava & Morin 1998; Chalcraft & Resetarits, personal

Table 1. Summary of predator population densities, total biomasses and average body sizes represented by the different experimental treatments

Treatment	Population biomass (g/tank)	Population density (no./tank)	Body size (g)
1 (control)	0·00	0	0
2	3·50	1	3·50
3	3·50	2	1·75
4	7·00	1	7·00
5	7·00	2	3·50

observation). Tanks had one of three different average body sizes of fish: 1·75 g, 3·5 g or 7 g and 3·5 g fish occurred in two treatments (one or two fish/1000 L) differing in total biomass (Table 1). Fish of 1·75 g, 3·5 g and 7 g are referred to as small, intermediate and large, respectively. We created an inverse relationship between body size and population density by manipulating independently the density and total biomass of predators, thus facilitating comparisons among populations with similar densities and biomasses of different sized predators. Furthermore, we can evaluate whether total biomass, density or their interaction cause predator populations to differ in impacts (Morin 1995). *Enneacanthus* were captured in the field and held in tanks similar to experimental tanks for approximately 1 week.

We conducted all procedures on a block by block basis to minimize variation within a block not attributable to treatments. Tanks were filled from a nearby pond and received 1 kg of leaf litter on 13–14 April 2000. Pond water was filtered through 2 mm mesh, allowing zooplankton, phytoplankton, periphyton and small invertebrates to pass, but excluding larger invertebrates and vertebrates. Each tank was covered with a tight-fitting screen lid to prevent unwanted colonization and to contain experimental animals. On 27 April 2000 we added 440 newly hatched *Rana* to each tank. One day after adding *Rana*, we assigned randomly one of the five treatments to each tank within a block.

Sixteen days after the experiment began, we drained all tanks and measured the wet mass (*Enneacanthus*) or snout–vent length (SVL) (*Rana*) of the remaining animals. The experiment was terminated because *Enneacanthus* is a voracious predator on tadpoles (Kurzava & Morin 1998; Chalcraft & Resetarits 2003a) and we wanted to ensure that some tadpoles remained in each tank to measure more accurately the rate of *Rana* population decline. The short duration also ensured that *Rana* was susceptible to predation in all treatments for the same period of time since *Rana* tadpoles can outgrow predators with smaller gapes. Previously, we (Chalcraft & Resetarits 2003b) demonstrated that differences in gape size played an important role in differentiating strong vs. weak effects on *Rana*. A longer experiment would not differentiate between rate of consumption or differences in the amount of time susceptible to predation.

To confirm that the smallest predators in our experiment were able to consume tadpoles, we conducted feeding trials in the laboratory between 23 and 30 June 2001 to determine if 1·75 g *Enneacanthus* could consume *Rana* of the size that survived in the mesocosms. We used four 38-L aquaria arranged in a linear array on a laboratory bench. Aquaria were filled with pond water filtered through 2 mm mesh. Black plastic covered aquaria walls to prevent fish from being disturbed by motion outside the aquaria. Twenty larval *Rana* of the size recovered in tanks with small fish in the tank experiment were added to each aquaria. We then assigned randomly one small *Enneacanthus* to one of each pair of aquaria (spatial block). No other materials were added to the aquaria to provide a refuge or to hinder the fish. After 48 h we counted the number of surviving *Rana*. We repeated this process three times to produce six replicates. Aquaria were cleaned thoroughly between trials and no fish or tadpoles were used twice. The amount of tadpole consumption by fish within a spatial block was calculated as the difference between the number of tadpoles surviving with and without fish.

RESPONSE VARIABLES AND STATISTICAL ANALYSES

We measured the impact of each population (PI) of fish on survivorship of *Rana* using the following equation:

$$\mathrm{PI} = \ln\left(\frac{E}{C}\right) \qquad \text{eqn 4}$$

where E is *Rana* survival in a particular fish treatment and C is *Rana* survival with no predators (Laska & Wootton 1998). E- and C-values were derived from tanks in the same block. Positive values indicate enhanced survival relative to controls while negative values indicate reduced survival. We also estimated per capita effects of predators within a tank by dividing eqn 4 by the number of predators (Laska & Wootton 1998). The TED of predator populations were estimated twice using eqns 1 and 2 with $b = 0{\cdot}75$ and $b = 0{\cdot}67$. Parameter a in eqn 1 was held constant in all cases as this does not affect the relative TED among populations in the same taxon.

We used ANOVA to determine whether fish populations of similar biomass or density differed in impacts on *Rana* survivorship. If differences in impact is qualitatively similar to differences in predator TED, allometric models predict that (i) populations with a higher biomass will have greater impacts and (ii) effect of density on predator impacts will be greater in high than low biomass populations (Fig. 1). It should be clear that this second prediction results not from density-dependence *per se* but rather from the non-linear relationship between body size and metabolic rate. We performed a linear regression to determine if the observed predator impact was predictable from the predator TED.

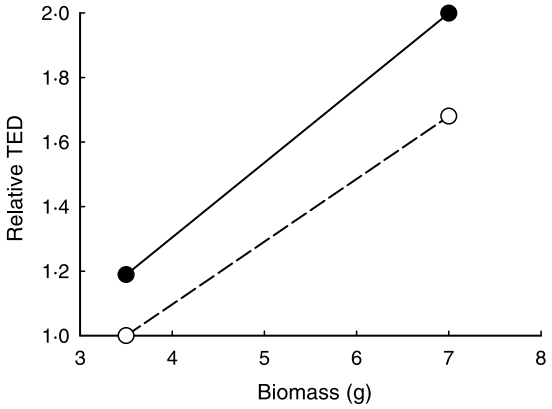

Fig. 1. Relative TED of the different predator populations used in this experiment. TED was calculated according to eqns 1 and 2 and standardized to populations with one intermediate fish. Open circles and dashed lines represent populations with one fish while filled circles and solid lines represent populations with two fish. Note that the difference in the elevation of points at 7 g is nearly twice that of the difference at 3·5 g. This interaction between density and biomass is indicative of the nonlinear relationship between body size and metabolic rate in the absence of density-dependent mechanisms.

We determined if density-dependence influenced per capita effects of fish in two ways. First, using an ANOVA we determined whether per capita effects of predators having the same body size (intermediate) was the same with one vs. two predators. Secondly, we compared slope estimates for regression lines (Zar 1974) of ln body size against per capita effect on *Rana* survivorship for each density ($n = 6$ for each density). Although only two body sizes were used in slope calculations for per capita effect of body size at each density, replication at each body size provided a reliable estimate of change in per capita effect per unit biomass. Slope estimates will be similar if the strength of density-dependence is the same for all body sizes. Allometric models also indicate the slope of the per capita impact –ln body size relationship should be equal to parameter b (i.e. 0·67 or 0·75).

Results

Enneacanthus had a negative effect on *Rana* survivorship (Table 2). Treatments with low fish biomass had the weakest effect (Fig. 2). At high biomass, two intermediate-sized fish had a greater effect on *Rana* survivorship than did a single large fish (Fig. 2). Total biomass was the primary factor causing predator populations to differ in their effects but density and the density–biomass interaction also explained a large proportion of variation (Table 2). Fish populations with low total biomass did not differ in their effects on *Rana* survivorship even though the populations differed in average body size and population density (Fig. 2). The impact of predator populations was correlated strongly with TED whether parameter b was equal to 0·75 ($F_{1,10} = 29{\cdot}495$, $P < 0{\cdot}001$, $R^2 = 0{\cdot}75$) or to 0·67 ($F_{1,10} = 39{\cdot}603$, $P < 0{\cdot}001$, $R^2 = 0{\cdot}80$) (Fig. 3).

A linear regression of predator per capita effect on ln fish body size indicates that larger predators have a greater per capita effect regardless of whether the population consists of one ($F_{1,4} = 11{\cdot}031$, $P = 0{\cdot}029$, $R^2 = 0{\cdot}73$) or two ($F_{1,4} = 123{\cdot}990$, $P < 0{\cdot}001$, $R^2 = 0{\cdot}97$) individuals (Fig. 4). Slope of the predator per capita effect–fish body size relationship, however, was steeper with two predators (–2·81 ± 0·25) than with one (–1·22 ± 0·37) ($t_8 = 11{\cdot}540$, $P < 0{\cdot}001$). The slope estimate was not different from either parameter b-value (0·75 and 0·67) used in metabolic models with one predator, but was steeper than both parameter b-values with two predators. When body size is held constant, per capita effect of intermediate-sized predators was greater at higher densities ($F_{1,2} = 148{\cdot}200$, $P = 0{\cdot}007$) (Fig. 4). If data for per capita effects of two small fish is included with regression data for one fish, slope of the relationship does not change (–1·08 ± 0·15) and explains a larger proportion of variation ($R^2 = 0{\cdot}89$). This suggests that per capita effects of small fish are not affected by presence of two fish to the same degree as in intermediate-sized fish.

The importance of density-dependence in populations with two intermediate-sized fish (i.e. change in the per capita effect with increasing density) suggests that the model describing the TED-population impact relationship may be inaccurate as differences in the strength of density-dependence among populations affects the slope of the relationship. To construct a model of the TED-population impact relationship without strong density-dependence, we performed a regression in which

Table 2. Results of factorial ANOVA to determine if predator populations having different average body sizes and population densities differ in their impact on the survivorship of *Rana*. The two factors of primary interest are total population biomass and population density. Percentage variation refers to the total amount of variation in predator impacts that is produced by the effect of total biomass, density and their interaction

Source	*SS*	d.f.	*F*	*P*	% Variation
Block	0·156	2	3·275	0·234	
Total biomass	17·419	1	729·857	< 0·001	55·7
Total biomass × block	0·106	2	2·229	0·310	
Density	6·767	1	283·534	< 0·001	21·6
Density × block	0·085	2	1·776	0·360	
Total biomass × density	6·678	1	279·814	< 0·001	21·4
Error	0·048	2			

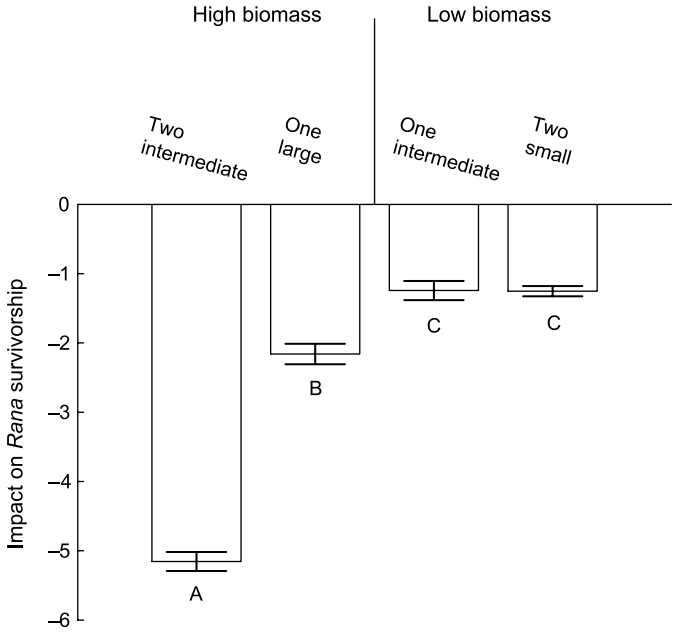

Fig. 2. Mean (± 1 SE) impact of predator populations on the survivorship of *Rana*. The four bars represents predator populations having different densities (one vs. two) and average body sizes (small vs. intermediate vs. large) High and low biomass refer to whether the fish population had a total biomass of 7 g or 3·5 g, respectively. Letters below the bars indicate which means are significantly different from each other. Pairs of means were compared using Bonferroni adjustments. $n = 3$ in all cases.

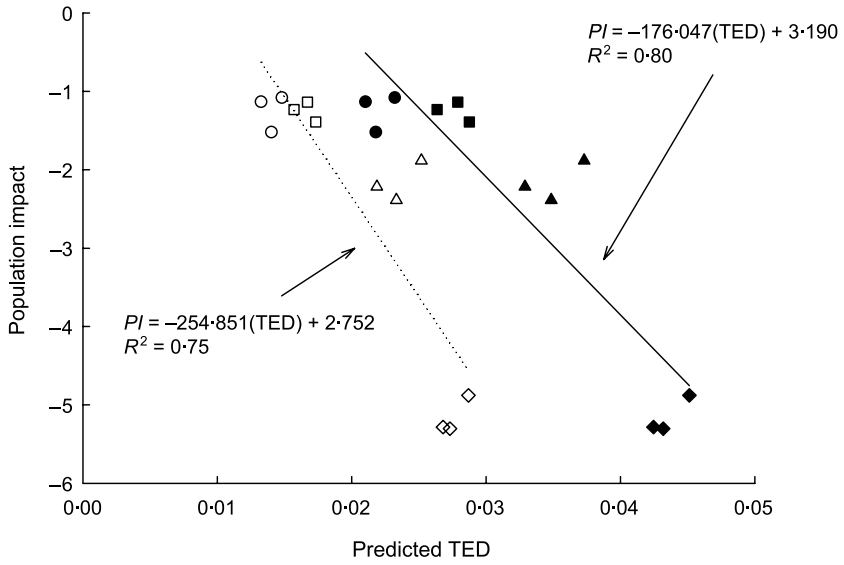

Fig. 3. Relationship between predicted TED and predator population impact (PI) on the survivorship of *Rana* when parameter b is equal to 0·67 (filled symbols) and – 0·75 (open symbols). Populations with one large fish, one intermediate-sized fish, two small fish or two intermediate-sized fish are represented by (▲, △), (●, ○) and (◆, ◇), respectively. The solid regression line is for conditions in which parameter b is equal to 0·67 while the dotted regression line is for conditions in which parameter b is equal to 0·75.

observed values for predator populations with two intermediate-sized fish were replaced with expected values based on lack of density-dependence. Expected impacts for two intermediate-sized fish were calculated by doubling the impact of one intermediate-sized fish in the same block. This additive model is appropriate to estimate the effect of multiple predator individuals with no density-dependence because it (i) assumes that the presence of one predator does not alter the per capita consumption rate of another and (ii) our measure of predator impact approximates instantaneous consumption rates due to the ln transformation (Billick & Case 1994; Wootton 1994; Sih, Englund & Wooster 1998).

Although TED predicts the impact of predator populations with weak density-dependence well (R^2 = 0·84 and 0·86 when parameter b = 0·67 and 0·75, respectively), removing density-dependence in populations with two intermediate-sized fish caused the slope of the relationship

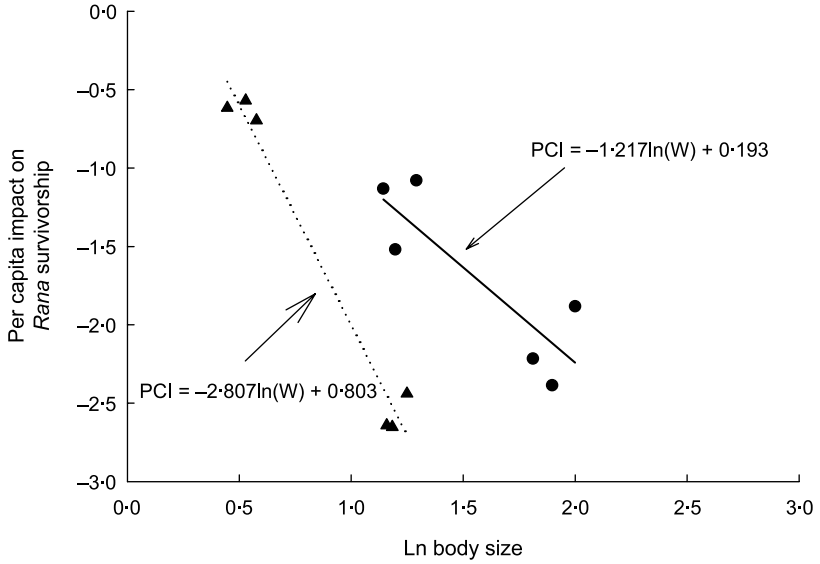

Fig. 4. Regression of the per capita impact (PCI) on the survivorship of *Rana* on the ln body size (W) when the population density of predators is equal to one (●, solid line) and two (▲, dotted line).

Table 3. Results of *t*-tests comparing the slopes for the relationship between population TED and population impact when density-dependence occurs or does not occur in populations with two intermediate-sized fish. The two different *b* parameter estimates used to calculate TED were 0·75 and 0·67

	Slope				
Parameter *b*-value	with density-dependence	without density-dependence	*t*	d.f.	*P*
0·75	–254·85	–95·13	12·289	20	< 0·001
0·67	–176·05	–61·69	15·034	20	< 0·001

between population impact and population TED to be significantly lower than when density-dependence was included (Table 3, Fig. 5a). To determine how much of the total variation in observed impacts results from variation in population TED alone, we calculated residual sums of squares ($SS_{residual}$) when the new regression model was applied to original data that included strong density-dependence (Fig. 5b). The proportion of the total variation in predator impacts that was attributable to TED alone is:

$$1 - \left(\frac{SS_{residual}}{SS_{total}} \right) \qquad \text{eqn 5}$$

where SS_{total} is the total sums of squares associated with variation in the observed impact of predator populations. Independent of strong density-dependent effects, TED accounted for 29% and 28% of the total variation in predator impacts when parameter *b* is 0·67 and 0·75, respectively. Thus, TED alone did not explain a large amount of variation in the impact of predator populations that differ in their strength of density-dependent effects whether parameter *b* was equal to 0·67 ($F_{1,10}$ = 4·099, $P > 0·10$) or 0·75 ($F_{1,10}$ = 3·940, $P > 0·10$)

Fish did not grow significantly during the experiment (Δ mass = 0·009 ± 0·007 g, t_{11} = 1·272, P = 0·229) and the laboratory feeding trials indicated that small fish could consume tadpoles of the size remaining in tanks with small fish [mean size (SVL) = 7·34 ± 0·09 mm, number consumed = 7·00 ± 2·46, t_5 = 2·842, P = 0·036]. Although per capita effect per day were higher for small fish in aquaria (–0·277 ± 0·122) than for small fish in the large tank experiment (–0·0392 ± 0·002), the difference was not significant (U = 15, N_1 = 6, N_2 = 3, P = 0·120).

Discussion

Two of our primary objectives were to determine whether differences among populations in average body size and density caused populations to differ in their effect on food resources and whether allometric models could predict the relative impact of different populations. Both variation in body size and population density caused predator populations of the same species to differ in their impacts on prey survivorship. Of the six pairwise comparisons among four different predator populations, only one suggested substitutability (two small fish and one intermediate fish). Although differences in total biomass explained a large amount of variation, effects of density and the density–total biomass interaction accounted for a comparable amount of variation in predator impacts. The significant interaction term indicates that knowledge of both population density and size structure is necessary to predict the impacts of predators. Differences in predator impacts did not result from differences in the time *Rana* was susceptible to predation; small fish were capable of consuming the surviving tadpoles. Furthermore, population TED did not change during the experiment; no fish died

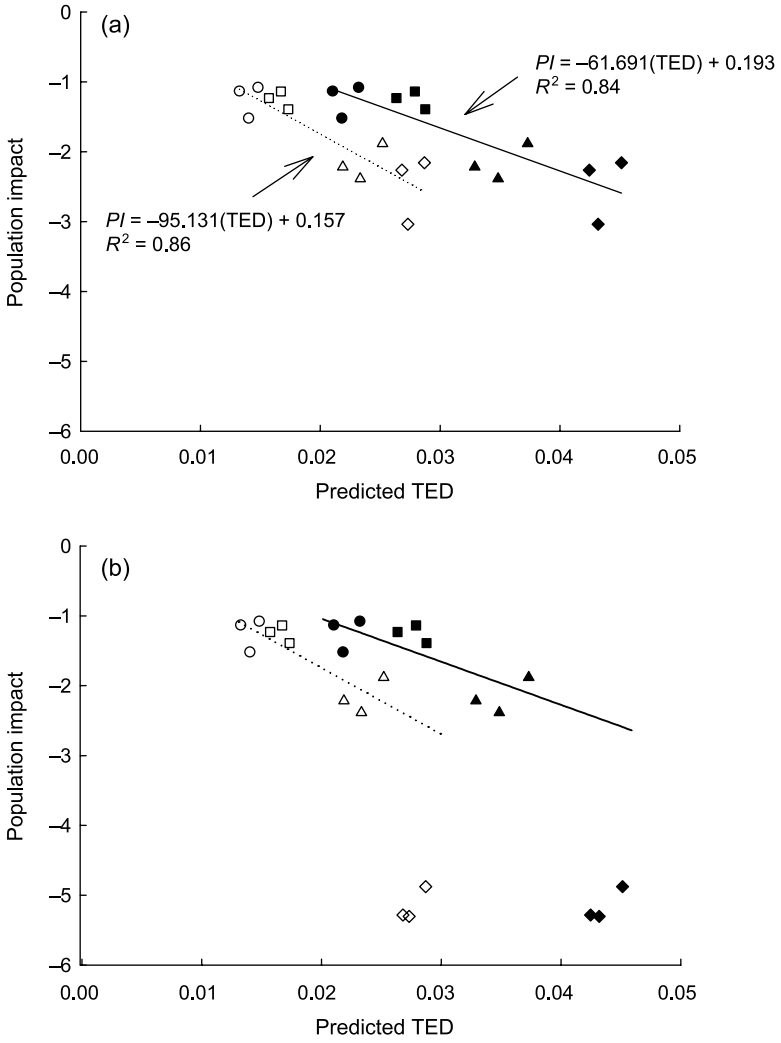

Fig. 5. Relationship between predicted TED and predator population impact (PI) on the survivorship of *Rana* when parameter *b* is equal to 0·67 (filled symbols) and 0·75 (open symbols). In (a) the impact of populations with two intermediate-sized fish was adjusted to remove the effect of strong density-dependence (see text for details). In (b) the regression model derived from (a) is applied to data in which strong density-dependence is present in populations with two intermediate-sized fish. Populations with one large fish, one intermediate-sized fish, two small fish or two intermediate-sized fish are represented by (▲, △), (●, ○), (■, □) and (◆, ◇), respectively. The solid regression line is for conditions in which parameter *b* is equal to 0·67 while the dotted regression line is for conditions in which parameter *b* is equal to 0·7.

and growth was minimal. These results indicate that an inverse relationship between population density and average body size can drive differences in predator impacts on prey. Populations consisting of smaller but more individuals can have impacts as large or larger than those of populations with larger individuals. These results are in qualitative agreement with the predictions of allometric models (Fig. 1).

The apparent success of allometric models in predicting the impact of predators is also supported by a strong association between TED and population impact. This point is similar to Ruesink & Srivastava's (2001) conclusion that the effect of a detritivore guild was predicted accurately based on guild TED. This strong association can be deceiving, however, when the slope of the TED–population impact relationship is greatly affected by density-dependence. As a result, populations with different body sizes but similar TEDs may differ in their impacts even if the equality of eqn 3 is satisfied because of differences in the intensity of density-dependence. Thus, use of allometric models to predict predator impacts appears limited when density-dependence is strong. Of course, if the strength of density-dependence is known, appropriate corrections can be made. More studies are necessary to evaluate the degree to which populations with identical TED but different responses to density vary in impacts on prey survival.

Our conclusion supports Ruesink's (2000) claim that strong density-dependence caused per capita effects of grazers under field conditions to be lower than in the laboratory. In contrast, however, we found that allometric models underestimate the effect of predator populations with strong density-dependence. In our system, intermediate-sized predators apparently facilitated each

other, leading to increased per capita consumption rate. Such facilitation is not uncommon, but the reason is not always clear (see review in Sih *et al.* 1998). Facilitation may not translate into increased growth, however, if increase in consumption rate compensates only for other energy costs (e.g. aggression, territoriality, etc.). Understanding conditions that generate enhanced or reduced consumption rates would be useful for predicting predator impacts.

A common practice in ecology is to standardize comparisons among different species or communities by maintaining density, biomass or TED constant (e.g. Morin 1983; Wilbur & Fauth 1990; Kurzava & Morin 1994, 1998; Hooper & Vitousek 1998; Srivastava & Lawton 1998; Ruesink 2000; Relyea 2001; Ruesink & Srivastava 2001; Schmitz & Suttle 2001; Chalcraft & Resetarits 2003a). Such attempts will not be effective, however, if even populations of the same species have different effects despite similar biomass, density or TED. Ecologists must recognize that such differences might result from group- (or species-) specific characteristics associated with body size and/or response to changing population density. Furthermore, standardization procedures may require experimental densities that are extreme, as the equality in eqn 3 is unlikely to hold for most populations because considerable variation in population density is not attributable to body size (review: Brown 1995; Brawn, Karr & Nichols 1995). Thus, species should be maintained at densities within the range observed in nature rather than using inappropriate densities to satisfy requirements of a model based on the measurements of individuals in isolation. TED may be an appropriate way to standardize comparisons when density-dependent effects are rather weak and densities fall within the natural range (e.g. Ruesink & Srivastava 2001). In such cases, eqn 3 provides an appropriate model to describe which populations will be substitutable on the basis of allometric relationships. Otherwise ecologists should be cautious in applying Damuth's rule of energetic equivalence. Hence, no single method of standardizing comparisons among groups of organisms is necessarily better as there will typically be confounding effects with either TED, body size or density-dependence.

Our study demonstrated two important features about the relationship between per capita consumption rate and body size. First, larger organisms had a greater per capita effect than smaller organisms. Although Travis *et al*. (1985) found only a small difference in predation rates of larger dragonfly naiads (compared to smaller naiads), our result is in agreement with numerous studies comparing effects of organisms with different body and/or gape sizes (e.g. Paine 1976; Morin 1983; Peters 1983; Fauth & Resetarits 1991; Kurzava & Morin 1994; Babbitt & Tanner 1998; Semlitsch & Gibbons 1988; Chalcraft & Resetarits 2003b). Many of these results, however, include effects attributable to differences in exposure time as a result of gape limitation (e.g. Morin 1983; Fauth & Resetarits 1991; Kurzava & Morin 1994; Babbitt & Tanner 1998; Chalcraft & Resetarits 2003b), which was not an issue in our study. We demonstrated that small predators have weaker per capita effects even when prey have not reached a size refuge, probably because small individuals have a lower total energy demand. In addition, small individuals may have greater handling times or be less efficient in capturing prey (Travis *et al*. 1985; Semlitsch & Gibbons 1988). Second, increasing population density may affect the per capita consumption rate of larger predators to a greater degree than smaller ones. This suggests that effects of density-dependence vary with body size. Thus, predicting effects based on TED may be complicated as effects of density-dependence and metabolic rate are interdependent.

The substitutability of populations depends on complex relationships between body size, population density and the strength of density-dependence. Given the restrictive conditions necessary to establish functional equivalence, even among different populations of the same species, functional equivalence should be rare in natural communities. The lack of functional equivalence among different populations or species may cause experimental studies to provide conflicting support for opposing models of trophic structure (e.g. the relative importance of top-down vs. bottom-up forces). Hence, ecologists need to consider the relationships between population density, metabolic rate and density-dependence within groups of organisms (e.g. predators) that they intend to manipulate experimentally. Our results indicate that to predict the consequences of biodiversity loss or species gain more effectively will require understanding how differences in average body size, population density and strength of density-dependence cause local populations to vary in their effects on ecological processes of interest.

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